Can jackdaws (*Corvus monedula*) select individuals based on their ability to help?

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Knowing the individual skills and competences of one's group members may be important for deciding from whom to learn (social learning), with whom to collaborate and whom to follow. We investigated whether 12 jackdaws could select conspecifics based on their helping skills, which had been exhibited in a previous context. The birds were tested in a blocked-exit-situation, where they could choose between two conspecifics, one of which could be recruited inside. One conspecific had previously displayed the ability to open the exit door whilst the other individual lacked the skill. The subjects showed a significant preference for the skilled conspecific if they had previously directly benefited from this skill. If they had merely observed the skilled (and non-skilled) individual opening (or failing to open) the exit door, they did not preferably choose the skilled conspecific. Taken together, these results suggest that jackdaws are capable of assessing other individuals' competence under certain circumstances.

1. Introduction

The question of whether non-human animals understand others' behaviour as guided by unobservable mental states, such as perceptions, intentions, desires and beliefs, i.e. whether animals form a human-like 'theory of mind' (ToM) (Premack & Woodruff 1978) remains contentious. *Informational* ToM (Premack 1988), one of the three components of a full-blown ToM, entails understanding that other individuals have beliefs or knowledge of specific facets of the world. Theoretically, the ability to reason about others' knowledge states (knowledge attribution) seems advantageous for social living species in several contexts of social life, such as competition over resources, cooperation, or social learning (see below). However, many social situations could be solved by reasoning about behaviour alone without the additional construal of superimposed mental states (Povinelli & Vonk 2004).

Hence, it is critical in the investigation of ToM in non-human animals to determine whether an animal has in fact acted based on its analysis of others'

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unobservable mental states or whether the same response could have been generated by non-mentalistic mechanisms, such as contingency-based learning, chaining (Epstein, Kirshnit, Lazna & Rubin 1984) or discriminative cues (Heyes 1998; Penn & Povinelli 2007; Povinelli & Vonk 2004).

Several approaches have been taken to investigate knowledge attribution in non-human animals, many of which suffer from methodological shortcomings or ecological invalidity (reviews by Heyes 1998; Penn & Povinelli 2007; Tomasello & Call 1997). One of the first studies to address the question of whether animals have a concept of knowledge was Povinelli and colleagues' (1990) classic guesser-knower experiment. In this paradigm, chimpanzees had to choose between two human experimenters, only one of whom had witnessed where the food was hidden, whilst the guesser had left the room during the hiding. The rationale behind this was that the two experimenters differed in their knowledge states of the whereabouts of a food reward, and that therefore the chimpanzees should address their begging to the knowledgeable person only. Having learnt to beg only from the experimenter who was present when the food was hidden consistently, the chimpanzees were tested in the critical transfer task. Here, the guesser remained in the room but could not witness the baiting because a bag or a bucket was covering her head. Although learning of discriminative cues and generalising simple rules could lead to 'false positives' in this task, the guesser-knower paradigm stands out as the first implementation of Heyes' (Heyes 1993, 1998) triangulation method, which consists of a discrimination training followed by transfer tasks that vary the perceptual but not the causal features (or vice versa) of the original task. The chimpanzees, however, failed this task, probably because begging for food and expecting others to share does not represent a naturalistic and ecologically valid situation for them.

Subsequently evidence has accumulated that at least chimpanzees (for review see Call & Tomasello 2008) as well as several corvid species (Bugnyar & Heinrich 2005; Bugnyar & Kotrschal 2004; for review on scrub jays see Clayton, Dally, & Emery 2007) seem to be capable of knowledge attribution. They all can take others' visual perspective and infer from their current or previous perceptual access what others know, hence relying on an understanding that 'seeing leads to knowing' (Gagliardi, Kirkpatrick-Steger, Thomas, Allen, & Blumberg 1995). It is likely that this ability is a cognitive adaptation to the competitive foraging and/or food caching situations encountered characteristically by these species, in which sensitivity to conspecifics' visual access to food confers great advantages. In fact, in the case of food-caching corvids the birds' reliance on stored food and high pilfering rates may have resulted in an evolutionary 'cognitive arms race' between cachers and pilferers (Bugnyar & Kotrschal 2002;

Dally, Clayton, et al. 2006), where individuals play both roles, with strong selection pressures towards an understanding of others' knowledge states.

In all studies that have investigated 'knowledge attribution' in non-human animals to date, knowledge could be inferred from what others have or have not seen (or heard), hence, from their perceptual access. This suggests that the species appear to have evolved some understanding that the perceptive act brings information (that was previously visible) to the mind. However, if we define knowledge operationally, as '(stored) information that can be used flexibly to achieve specific goals if appropriate', this covers just some aspect of potentially relevant knowledge. There are other forms of knowledge that cannot be tied to single perceptive events, but that are gradually acquired through learning, experience, association or reasoning. Such knowledge may range from social knowledge, e.g. knowing third party relationships (Paz-y-Mino, Bond, Kamil, & Balda 2004), routes to foraging sites (Biro, Sumpter, Meade, & Guilford 2006; Couzin, Krause, Franks, & Levin 2005), or specialised foraging techniques, such as tool use (Hunt & Gray 2003; Nagell, Olguin, & Tomasello 1993). Identifying skills one does not have oneself in other group-members may be of importance for social learning, cooperation and group decision-making; the ability to assess the skills and competences of others to choose suitable co-operators, tutors or guides, etc., accordingly, seems highly advantageous in group living animals. However, there are very few studies to date that investigate whether animals may take others' skills and competences into account in such situations. For example, in experimental situations macaques eventually responded to individuals with particular food production skills after having scrounged food from them repeatedly (Stammbach 1988), and chimpanzees choose between efficient and less efficient conspecific collaborators based on their previous experiences with those individuals in a cooperative task (Melis, Hare, & Tomasello 2006).

We investigated whether jackdaws (*Corvus monedula*), a social, non-caching corvid species, could differentiate between skilled and ignorant individuals and select the appropriate individual to aid in a problem situation. Jackdaws have been shown to be sensitive to others' knowledge states depending on their previous visual access in a competitive foraging situation (von Bayern 2008). Hence, we devised an experiment in which a jackdaw's knowledge state could not be inferred from its current or previous perceptual access (i.e. what it had or had not seen), but from other 'observables', namely certain skills exhibited by that individual or not (i.e. what it could or could not do). Adopting the general knower-guesser paradigm (Povinelli et al. 1990), but using conspecifics instead of human experimenters and testing the subjects in two critical transfer tests, we chose a scenario in which the subject was placed into a box with a blocked exit. In this situation, the subject could choose between two individuals, one of whom had the skill of opening an 'exit door' whilst the other individual was ignorant of this mechanism.

The experiment consisted of a general preparatory training phase followed by two specific training stages with a subsequent transfer test in each. The first transfer test, the 'experiential' test, examined whether jackdaws were capable of choosing a skilled individual together with whom they had previously left the box, i.e. whether they could use their former positive associations with that skilled individual in the choice situation of the test, which could be achieved by associative learning. The second critical transfer test, the 'observational' test, investigated whether the jackdaws could also identify and choose a skilled individual based on their former observations of this individual leaving the box (without subjective positive associations), hence posing higher cognitive demands than the former transfer test.

2. Methods

2.1 Subjects

Subjects were 12 hand-raised jackdaws (4 males, 8 females). The group was composed of 4 stable heterosexual pairs, 1 female-female pair and 2 females that were solitary. Ten individuals were 2 yrs old; the remaining 2 birds were 1 and 3 yrs old. The jackdaws were group-housed in a spacious out-door aviary (10 m 12 m) with associated testing compartments. They were fed a variable ad-lib diet consisting of meat, soaked cat-biscuits, a meat-curd-rice formula, seeds, cereals, fruit, and dried insects.

2.2 Experimental groups

The individuals were divided into two groups (A & B for the experiential condition and C & D for the observational condition). Eight jackdaws were in Group A/C. Group B/D consisted of the 4 individuals that had acted as the Knower in Group A/C before, and were tested once the experiment with Group A/C had been completed. Individuals were divided into three categories; Subjects, Ignorants and Knowers. All Subjects also functioned as Ignorant during the training of other subjects (see Table 1). During training and testing, the Subject was placed in a chamber together with a conspecific (Ignorant or Knower) that was not their mate. Since aggression can occur when two adult jackdaws are in a confined space together, preliminary tests established which individuals were compatible.

The dominance status and sex of these two birds (Knower and Ignorant) were kept as balanced as possible with the available combinations across subjects (see Table 1). Five subjects were tested with a Knower that was of a higher relative

Table 1. The subjects and the respective individuals in the Knower and Ignorant role in transfer test 1. Individuals of Group B were used as Knowers for Group A and vice versa (the individuals of Group A that are shaded dark played the K role for Group B). The rows of the table give the details (i.e. name, sex) for the 12 subjects and for the respective Knowers and Ignorants, and the Subject's relative dominance status (Dom.) to both of them. The fields in the Dom. columns filled grey denote the lower-ranking individual if the Knower and Ignorant differ in their relative dominance status to the Subject (the ratio was balanced across subjects)

Group	Subject	Sex	Knower	Sex	Dom.	Ignorant	Sex	Dom.
A	Leonhard	♂	Zorro	♂	>=	Tschok	♂	>=
A	Mucke	♀	Spinni	♂	>	Tschok	♂	>
A	Chocolate	♀	Anders	♀	>=	Leonhard	♂	<
A	Tschok	♂	Karacho	♀	>	Leonhard	♂	<=
A	Csoka	♀	Anders	♀	>	Franzi	♀	=
A	Magret	♀	Karacho	♀	>	Traute	♀	=
A	Franzi	♀	Zorro	♂	<	Csoka	♀	=
A	Traute	♀	Spinni	♂	<=	Magret	♀	=
B	Karacho	♀	Traute	♀	<	Anders	♀	=
B	Anders	♀	Traute	♀	<	Karacho	♀	=
B	Spinni	♂	Magret	♀	>	Zorro	♂	=
B	Zorro	♂	Magret	♀	<	Spinni	♂	=

dominance status than the Ignorant, while five subjects experienced the opposite; for two subjects both Knower and Ignorant were lower-ranking. Six Subjects were tested with a Knower and Ignorant of the same sex, whilst in six cases, Ignorant and Knower were of a different sex (4/6 cases, the Knower was female and 2/6 cases the Knower was male).

2.3 Experimental set-up

The experiment was conducted in a 150 cm 45 cm 50 cm test-box consisting of three consecutive 50 cm 45 cm 50 cm chambers (A, B & C) divided by wire-mesh guillotine doors (see Figure 1). The middle chamber B was divided into two equally sized adjacent compartments (B_L = on the left and B_R = on the right, seen from C). The first chamber A served as an entrance to either compartment of the middle chamber (B_L & B_R).

The third chamber C, the actual test compartment, was connected to the two compartments B_L & B_R of the middle chamber B by two same-sized transparent Plexi-glass doors, which could be opened by lifting levers from inside the test compartment (Figure 2).

A wire-mesh guillotine door covered the levers in front of the Plexi-glass doors when lowered. This allowed the experimenter to control the subject's access

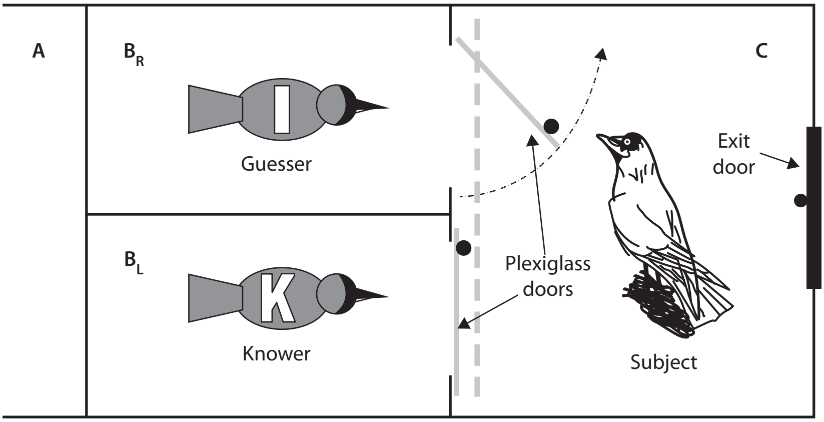

Figure 1. Schematic overhead view of the experimental setup in the test box (consisting of 3 adjacent compartments A, B & C). The broken line symbolises the wire-mesh guillotine door that could be pulled up to allow the subject access to the two opening levers (symbolised here as the twoblackdots) on the Plexi-glass doors to B_L & B_R. The dot at the exit door represents the opening mechanism of the exit

Figure 2. 1. The opening mechanism of the two Plexi-glass doors in the test compartment C. The two arrows mark the two levers that can be lifted to open either of the doors. 2. The doors in an opened state. Once the lever is lifted the door is pulled open by a stretched rubber ribbon. 3. View from the entrance into the 2 compartments of the middle chamber B, in which K and I were placed

to the levers. Once a lever was lifted and the respective door opened, the other door was immediately blocked by a mechanism operated by the experimenter. Therefore, just one door could be opened at one time.

A video camera (Sony DVD Camcorder) was mounted to the back wall of the box and focused on the two Plexi-glass doors between C and B. On the back wall of C was the exit door leading into the aviary: a round shaped falling door which opened upon operating a specific mechanism. For the experiential transfer training, a specific wooden plug had to be pulled out, which could be blocked

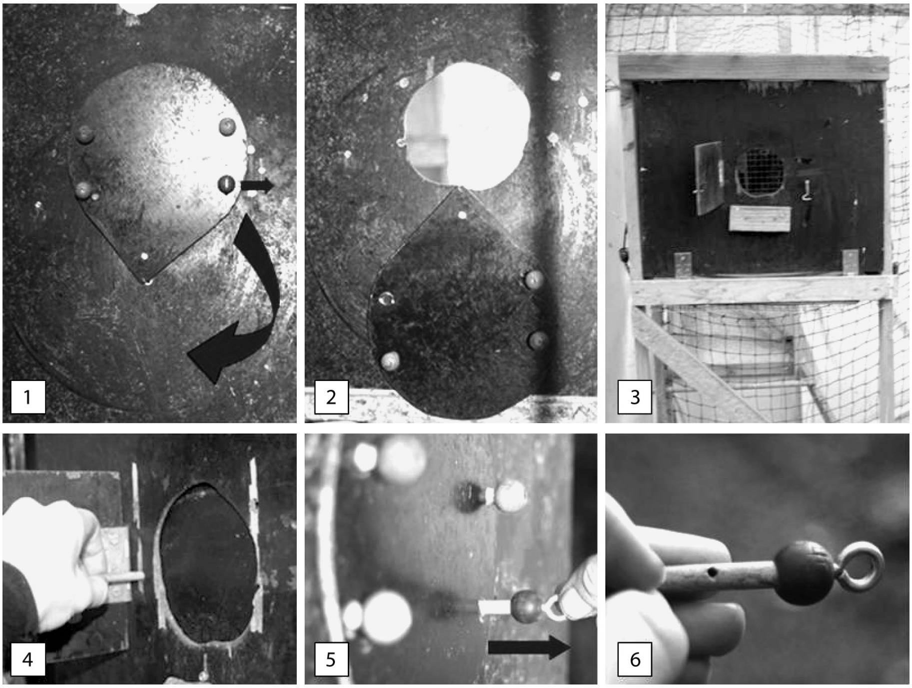

Figure 3. 1. Exit door seen from within the C in closed state. If the red plug (marked by the horizontal arrow) was pulled out, the door fell open. 2. Exit door open. 3. Test compartment C seen from outside. 4. Closed exit door seen from outside; the plug stuck through the back wall of the test compartment and could be blocked by a nail. 5. Close-up of the red (functional) and the fake (non-functional) plugs in the exit door. 6. The red plug with a hole through which a nail can be stuck

by the experimenter at any time (Figure 3). Additional fake plugs were added as distracters in order to make the mechanism less obvious to the birds (red and on the right side of the exit for Knowers in Group A; white and on the left side of the exit for Knowers in Group B). For the observational transfer training, the exit door could be opened using a new mechanism of comparable difficulty. Here the Knowers were trained to pull down a wire handle (for Group C, the wire handle was green and on the right, for Group D it was grey and on the left).

2.4 Experimental procedure

The study consisted of two conditions, (1) the experiential transfer test and (2) the observational transfer test, which were both preceded by a training phase. First, Groups A and B were tested in the experiential transfer test, then the birds were newly distributed into Groups C and D with different Knowers and tested in the observational transfer test. Because the exit door mechanisms were different in the experiential and observational conditions, the birds went through further Knower-Ignorant training before the observational transfer training phase began.

2.5 Training stages

The test trials were preceded by three training stages: (a) Double-Door training including all birds, (b) Knower-Ignorant training including (i) Open-Exit training for the Knowers and (ii) Closed-Exit training for Subjects and Ignorants, and (c) (Conditional) Discrimination Training for the Subjects (see Table 2 for an overview).

Table 2. Overview over the different training stages: K = Knower and I = Ignorant

Training step	**Aim/content of the training**	**Number of trials**
a. Double-door training	Pre-training: learn to open the doors	Variable
	Learn to open one specific door	30–40 training trials (sides counterbalanced)
	Training: Open correct door to retrieve food (+ learn that only one door can be opened)	30–40 training trials (sides counterbalanced)
	Open correct door to be with partner (release after 4 min.)	10 training trials (sides counterbalanced)
	Open correct door to retrieve food	10 further training trials (refresh)
b. Knower-Ignorant training	Knower: Learn to open the exit door	variable
	Open exit door and leave C	16 training trials
	Ignorant/Subject: Experience that they cannot free themselves from c (release after 6 min.)	10
c. (Conditional) Discrimination training	Subject: encaged in C with K (K opens door within 1 min.)	7
	Encaged in C with I (release after 6 min.)	7
Transfer test 1: *experiential*	Subject: Choice between K and I	1(–2) (2nd trial was not counted)
Transfer test 2: *observational*	Subject: Choice between a new K and a new I (after having gone through a *new* discrimination training)	1

2.5.1 *a. Double-door training*

Prior to the experiment, all individuals went through an introductory training stage, during which they learned (a) to operate the levers of the two Plexi-glass doors and (b) that only one of these two doors could be opened at a time (i.e. after one door had been opened, the other door was blocked). This training was achieved in four steps.

(i) First, the jackdaws learned to push the levers up to open the doors in order to leave the test box. (ii) Second, the jackdaws learned that only the correct door, which led to B containing food, would open. The other door was blocked and a novel object, e.g. an empty bottle or can, a slightly aversive stimulus, was placed in the compartment that was blocked (the aversive stimulus was introduced because several birds were persistently indifferent as to which door they tried to open). The subject was released after it had opened the correct door (to B_L or B_R) and touched the food (which took 5 minutes maximum). The correct side was alternated pseudo randomly using a counterbalanced design. Between 16–20 trials per bird were conducted for each side. (iii) In the third step, both doors could be opened after the guillotine door was raised giving them access to the two levers, but after the Subject had made its choice, the other respective door was blocked immediately; the birds therefore could learn that their first choice was important. If the birds opened the wrong compartment, the correct door was blocked and the bird stayed in C for 4 minutes until it was released through the back wall flap of C (the entire back wall of C could be opened by the experimenter). If the choice of door was correct, the bird could take the food reward and was released 1 minute later. Each bird was given 16–20 training trials on each side. (iv) Having learnt to choose the door of the baited chamber, the subjects were now trained to choose between two conspecifics placed in B_L & B_R respectively, in order to prepare them for the test conditions. Each bird participated in 10 practice trials in which they could open the door leading either to their respective mate (or affiliate) or to a non-affiliate. The sides (B_L & B_R) of mate/affiliate and non-affiliate were exchanged alternately across trials. Once the subject had opened one of the two doors, the selected bird could enter C and was released from there (through the back wall flap of C) together with the subject after a further 4 minutes. This practice was important because the birds needed to experience the consequences of their actions, not just with regard to food but also to conspecifics. They had to learn that they could affect which individual could enter the test chamber (jackdaws are capable of visually distinguishing between their partner and a non-affiliate; von Bayern 2008). (v) After this experience, the food-training trials were resumed and the birds experienced 10 extra refresh trials before proceeding to the next training step, the Knower/Ignorant training.

2.5.2 *b. Knower-ignorant training (K/I training)*

Throughout K/I-training, Knowers were first taught to open the exit door (wooden plug in experiential condition, wire handle in observational condition) and then completed 16 training trials (Open-Exit training). In contrast, Subjects (most of which also played I in the same experiment) experienced 10 trials in which they were locked in C with the exit closed for 6 minutes (Closed-Exit training) after which the experimenter opened the flap back wall, i.e. the entire back wall of C (not just the exit door, to make it obvious that the human had freed the subjects). During Ignorant-training, the exit door mechanism, i.e. the plug or the handle, was blocked to avoid the birds learning how to open the door by trial and error.

2.5.3 *c. (Conditional) Discrimination training*

Once the birds had completed the preceding training, the Subjects went through the final stage (discrimination training), which prepared them for the actual transfer tests. Throughout discrimination training, each S had seven sessions with their respective Knower and seven sessions with the Ignorant (Ignorant and Knower were different individuals in the discrimination training for the experiential and observational transfer tests, respectively). Discrimination training for the experiential and observational transfer tests differed in one critical aspect. The experiential discrimination training was *conditional*, whereas the observational discrimination training was not (or to a lesser extent, as discussed below). In the experiential training, the Subject was placed *together* with (alternately) the Knower or the Ignorant in C. Being with the Knower, the Subject experienced seven trials of the Knower opening the exit door so that both birds could leave the box (usually within 1 minute). Being with the Ignorant, the Subject experienced seven trials remaining in the test compartment for 6 minutes before both birds were released by the experimenter opening the back wall flap of C. By contrast, during the observational discrimination training, the Subject was placed in the middle chamber B and could *observe* either the Knower or the Ignorant in C. The Knower usually opened the exit door and left C within 1 minute while the I remained in C for 5 minutes until it was released through the back wall flap of C by the experimenter. The Subject had to wait in B_L or B_R (the sides were counterbalanced and pseudo randomised so that the Subjects would not develop a preference for B_L or B_R) in both cases for 6 minutes until it was released by the experimenter through the side flap door of B_L or B_R. Releasing the Subject through a different door (and side) than the one that Knower and the Ignorant went out through was important, because the subjects should experience their release as independent of that of the Knower and the Ignorant.

2.6 Transfer test

Following the last training step, the discrimination training, each Subject was tested in a critical transfer test in which Knower and Ignorant were in B_L and B_R. The Subjects in C could let either the Knower or the Ignorant in by opening the appropriate Plexi-glass door. The Knower-side was pseudo randomised and counterbalanced across birds and across the two transfer tests. In the experiential transfer test, all subjects were tested twice, with the Knower on one side in the first test and on the other side in the second test. For half of the subjects, the Knower was on the left in the first trial and on the right in the second trial. For the other half of subjects, the situation was reversed. The observational transfer test comprised just a single trial.

2.7 Scoring and statistical analysis

From the video tape we scored whether the Subject opened the door of the Knower or the Ignorant. In addition, we recorded which lever the Subject operated first. If the Subject attempted to open a Plexi-glass door by pushing the lever up or rattled the lever without success, this was counted as a choice. One-tailed binomial tests were conducted (assuming 50% chance of choosing either side) to assess whether there was a statistically significant tendency to choose Knower using the statistical tables in Zar (1999). If any preference, hence a divergence from random choice, were to be expected *a priori,* it should be for the Knower, because it would cause the exit door to open faster. Therefore one-tailed tests were used in this analysis. Each test was analysed individually. Additionally, a two-tailed 2 2 McNemar's test for paired samples of dichotomous data (applying the binomial test for the calculation of P(X) as suggested by Zar 1999) compared the outcome of the birds' choices in the two transfer tests directly. Two-tailed Fisher's exact tests were conducted to compare the choices of males and females and the effect of dominance rank of Knower and Ignorant. The significance level α was set at $p = 0.05$ for all analyses.

3. **Results**

3.1 Experiential transfer test

Eight out of 12 birds chose the Knower in the first trial; thus the preference of Knower across subjects was not significant (one-tailed binomial test; $n = 12$; $p = 0.19$). However, two individuals (Mucke and Anders) had to be retested with a new

Knower because their original Knowers (Spinni and Traute, respectively) had started to behave aggressively towards these Subjects during the last training sessions, attacking and chasing the Subject around before opening the exit, thus confounding the prediction for Subject to choose the Knower. When new trials of those two subjects were considered instead of their initial trials, the results were significant with 10 out of 12 birds choosing the Knower (one-tailed binomial test; n = 12; p = 0.016). In the second trial, there was a non-significant trend to choose the Knower, as 9 out of 12 subjects opened the Knower door (one-tailed binomial test, n = 12; p = 0.054). Pooled together, trial 1 and 2 differed significantly from chance (one-tailed binomial test; n = 24; p = 0.0033). The results are presented in Table 3.

Table 3. Results of the experiential and observational transfer tests. The 1st letter in column 1 denotes the Group in the experiential test, and the 2nd letter the Group in the observational test. The plus sign indicates that the Knower (=K) was chosen; a zero indicates that the Ignorant bird (=I) was chosen. The two plus signs in bold indicate the two individuals that were retested. For the experiential test, the results of both tests are reported (although the 1st test was the critical test). Column 4 displays the results across the 2 experiential trials, whilst Column 6 summarises the performance of the birds in both the experiential and observational transfer tests. 2 = K was chosen in both tests; 1 = K was chosenin one of the tests; 0 = only I was chosen

Group	**Subject**	**experiential**		**#K chosen in experiential trials 1+2**	**observational**	**#K chosen in experiential & observational**
		trial 1	**(trial 2)**			
A/C	Leonhard	+	+	2	+	3
A/C	Mucke	+	+	2	+	3
A/D	Chocolate	0	+	1	0	1
A/C	Tschok	+	0	1	+	2
A/C	Csoka	+	+	2	0	2
A/D	Magret	+	+	2	0	2
A/C	Franzi	+	0	1	0	1
A/D	Traute	0	+	1	0	1
B/C	Karacho	+	0	1	+	2
B/D	Anders	+	+	2	o	2
B/C	Spinni	+	+	2	0	2
B/C	Zorro	+	+	2	0	2
	n=12	10/12	9/12	19/24	4/12	23/36

3.2 Observational transfer test

The observational transfer test was not significant, with only 4 out of 12 birds choosing the Knower (one-tailed binomial test; n = 12; p = 0.81; Table 3).

A McNemar's test revealed a significant difference between the experiential and observational transfer tests (McNemar's test; $n = 5$; $X^2 = 4.1667$; $p = 0.016$).

3.3 Sex and rank effects

There were no significant differences between the test outcomes of females or males in either of the transfer tests (Fisher Exact test; $n = 12$; experiential: $m_1 = 2$; $m_2 = 4$; $p \geq 0.5$; observational: $m_1 = 4$; $m_2 = 4$; $p \geq 0.5$) or the test outcomes depending on the relative rank of Knower and Guesser (Fisher Exact test; $n = 20$; $m_1 = 5$; $m_2 = 10$; $p \geq 0.5$).

4. Discussion

The aim of this study was to test whether the jackdaws could identify a skilled individual based on their previous experience or observation of that individual practising the skill, and whether they could recruit that individual in a problem-solving situation in which this skill was needed. Gauging the skills of others and recognising individuals with particular competences may play a role in social learning, cooperation and group decisions because animals may evolve the ability to decide from whom to learn (Laland 2004), whom to teach (Hoppitt et al. 2008), with whom to cooperate (Melis et al. 2006), and whom to follow (Biro et al. 2006; Couzin et al. 2005). So far, there is little experimental evidence that animals may purposefully choose their tutors, co-operators and leaders based on their skills (Melis et al. 2006) and, similarly, that animals may selectively direct their teaching efforts at inexperienced individuals (Hoppitt et al. 2008).

Our results suggest that jackdaws were able to select the skilled individual (the Knower) if they previously had directly *experienced*, i.e. benefited from their actions, as opposed to if they had just *observed* them. Consequently, several questions arise; did the subjects in the experiential transfer test differentiate between the knowledge states of Knower or Ignorant, or was their choice determined by other criteria? Why did the birds fail to solve the second, observational transfer test?

The design of this experiment aimed to expose the underlying cognitive processes of 'skill attribution', i.e. an understanding of what others can and cannot do. It applied Heyes' triangulation method (Heyes 1993, 1998) with two modifications. First, there were *two* transfer tests of *ascending* cognitive complexity. Whilst the simpler experiential transfer test was preceded by conditional discrimination training with differential reinforcement, the discrimination training for the cognitively more demanding observational transfer test involved non-reinforced *observations* of the Knower practising its skill. A similar design, where subjects received distinctive pre-trainings that resulted in different cognitive complexity of the subsequent critical test, had been used before by von Bayern et al. (2009). However, in contrast to the current experiment, subjects were assigned to differently pre-trained groups before being tested in the same task. Second, in a further difference, the discrimination training in the current study in itself was passive for both conditions; it did not involve an active choice task like Povinelli et al.'s (1990) knower-guesser experiment. Our subjects were presented with a choice for the first time only in the transfer test following this training. To make an appropriate decision, the animals had to use the experience they had gained during training, and apply it in a novel situation.

The preference for the Knower in the first experiential transfer test need not necessarily involve mental state attribution, i.e. an understanding that the Knower knows how to open the exit while the Ignorant does not. It is possible to explain the results by an associative account (Heyes 1998). The subject may have associated the identity of the Knower with the positive experience during the discrimination training of being rapidly released from the box when being with the Knower. In contrast, the Ignorant may have been associated with a longer stay in the box during the discrimination training and therefore might have been avoided. The different states previously experienced with the two individuals therefore could have affected the subject at the time of choice. The finding from the experiential transfer test compares with the study of Melis et al. (2006) in which chimpanzees had a choice between an efficient and a less efficient conspecific collaborator based on their previous experiences with those individuals in a cooperative task. Like the jackdaws in our experiment, the chimpanzees spontaneously opened the door for the efficient individual. Consequently, the chimpanzees' choice of collaborator could have been explained by positive associations with the more efficient individual. However, irrespective of the underlying mechanism that influenced the decision making, the fact that the subject spontaneously and actively let the appropriate skilled individual into C at first trial is interesting. Another possible explanation for the jackdaws' spontaneous opening of the door for the Knower (or Ignorant) could be a chaining mechanism, because the doors may have become conditioned reinforcers (Epstein, et al. 1984) through their association with food during the previous double-door training phase, hence prompting the subjects to choose a door in the new choice situation between two conspecifics.

The negative result of the second, observational transfer test indicates that directly experiencing the beneficial effect of the Knower's skill was necessary for the subjects to recognise its relevance in the test situation. It also suggests that the second transfer test may pose cognitive demands that are too high. Observing an action seems to be cognitively more demanding than directly experiencing or participating in an action. It has been suggested that young children fail in standard false belief tasks because they are required to take a third-person perspective rather than interacting with second-persons (Gallagher 2005).

The finding that the jackdaws required direct experience of the Knower's skill relates to Stammbach's study on longtailed Macaques (*Macaca fascicularis*), which reported that monkeys assess the specialised skills of others through experiencing the benefits of their actions. Stammbach trained low-ranking individuals to produce food for the group by operating a feeding apparatus in a special way. The other group-members gradually learnt that they benefited from allowing the skilled individual access to the apparatus and suppressing their own attempts. Most importantly, the status of such skilled food-producers changed as several individuals began to affiliate with them (Stammbach 1988).

There might be alternative reasons why the jackdaws failed to choose the Knower in the observational transfer test. First, it is possible that unintended differential reinforcement during the discrimination training, which might have conditioned the subjects negatively towards the Knower, confounded the results. The jackdaws might have perceived staying in the box alone after the Knower had liberated itself as frustrating compared to being in the box while another bird, the Ignorant, was present. Thus, the negative association could have resulted in a misconception of the task: Instead of seeking a solution for the closed exit, the birds' choice criterion may have been to avoid being in the box alone or the negative association of being abandoned by the Knower. A second reason for their failure could be lack of attention during the discrimination training. The non-affiliated birds in the neighbouring compartment may not have been relevant to the subjects so they did not pay attention to the Ignorant's or Knower's behaviour. During the discrimination training for transfer test one, in contrast, the birds were compelled to witness the behaviour of Knower and Ignorant because they stayed in the same compartment.

It is also possible that the jackdaws perform poorly in the 'observational' condition because, unlike New Caledonian crows (*Corvus moneludoides*) (Bluff, Weir, Rutz, Wimpenny, & Kacelnik 2007), social learning may not be ecologically relevant in their natural environment. Like rooks (*Corvus frugilegus*), jackdaws are attracted to objects and locations with which others are interacting (Dally, Clayton & Emery 2008; Schwab, Bugnyar, & Kotrschal 2007; Schwab, Bugnyar, Schloegl, & Kotrschal 2008), but they may be poor at forms of social learning more sophisticated than local enhancement (Federspiel et al. in preparation; Bird & Emery, in preparation).

Interpreting the jackdaws' success in the experimental and failure in the observational task in terms of its cognitive underpinnings is therefore not easy. Passing the first transfer suggests that the jackdaws understood which individual knew how to open the door, but it is equally possible that the subjects merely learnt to associate that individual with a quick release. Failure in the second transfer is consistent with an associative learning account, but it remains possible that the birds failed because they were not attentive to the behaviour of the Ignorant and the Knower. However, one may conclude from the first transfer that the jackdaws remembered the actions of the two individuals, i.e. who did what previously, without necessarily reasoning about their knowledge states. They could have chosen the bird that had previously opened the door because they may have expected it to *act as before* in the same situation, rather than attributing 'know-how'. One could call this an understanding of other individuals as agents with the potential for certain action, which can be used for predicting their behaviour. While it may be important to understand that an individual that has seen a piece of food knows *that* food is there, it appears less crucial to understand that an individual that could open a door knows *how* to open doors (i.e. what sequence of actions need to be carried out when confronted with a closed door). In the latter case, recalling the behaviour of the individual (i.e. that it did open a door) is sufficient for predicting its future behaviour in the same context. Philosophers have traditionally discriminated between knowing *how* and knowing *that*. The former, also referred to as procedural knowledge, is different from other kinds of knowledge, such as declarative knowledge, in that it can be directly applied to a task, such as opening a door. For instance, the procedural knowledge one uses to open a door differs from the declarative knowledge one possesses about the mechanisms and features of a door.

In conclusion, this experiment demonstrates that jackdaws are sensitive to others' previous actions and that they can select conspecifics according to their skills, but it is not clear what are the underlying mechanisms of their choice, whether based on their former positive associations with the birds or a more complex reasoning process, involving a memory of others' actions that can be used to anticipate their behaviour.

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